Tail walking in a bottlenose dolphin community: The rise and fall of an arbitrary cultural "fad"

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ABSTRACT

Social learning of adaptive behaviour is widespread in animal populations, but the spread of arbitrary behaviours is less common. Here we describe the rise and fall of a behaviour called tail walking, where a dolphin forces the majority of its body vertically out of the water and maintains the position by vigourously pumping its tail, in a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). The behaviour was introduced into the wild following the rehabilitation of a wild female individual, Billie, who was temporarily co-housed with trained dolphins in a dolphinarium. This individual was sighted performing the behaviour seven years after her 1988 release, as was one other female dolphin, named Wave. Initial production of the behaviour was rare, but following Billie's death two decades after her release, Wave began producing the behaviour at much higher rates, and several other dolphins in the community were subsequently sighted performing the behaviour. Social learning is the most likely mechanism for the introduction and spread of this unusual behaviour, which has no known adaptive function. These observations demonstrate the potential strength of the capacity for spontaneous imitation in bottlenose dolphins, and help explain the origin and spread of foraging specialisations observed in multiple populations of this genus.

KEYWORDS

Social learning; Cultural transmission; Cetacean; Bottlenose dolphin

BACKGROUND

The social learning of behaviour has been studied in a range of taxa, including primates [1], birds [2], fish [3] and insects [4]. When socially-learned behaviour persists long enough to become common within a group or population for some period of time, it becomes a cultural tradition [5]. In cetaceans, for example, “sponging” by bottlenose dolphins [6], prey specialisation in orca [7], and the spread of lobtail feeding in humpback whales [8] all appear to rely on social learning. However, these behaviours are associated with an obvious biological function - in these examples, foraging.

Examples of cultural behaviours with no obvious biological function have been described in primates. For example, capuchin monkeys have social behaviour traditions, such as the ‘finger-in-eye game’ [9]. It does not follow that these traditions serve no adaptive social function simply because it is not obvious and we cannot currently identify it, but they do appear to have a qualitatively different role compared to behaviours that have more obvious adaptive function, such as foraging. Some apparently arbitrary traditions can also be transient – for example, stone handling in a community of Japanese macaques has persisted for many years, but specific variants of the behaviour emerge and then disappear, and researchers refer to these as “fads” [10]. The practice of carrying dead salmon adopted for a few weeks by a community of orcas in Puget Sound has also been described as a fad [11].

In human culture, such arbitrary traits can acquire significance as symbolic ethnic markers [12]. Determining the social role and potential fitness advantage of such cultural behaviours in non-humans, especially when they are ephemeral and arbitrary in nature, remains a challenge. Therefore, documenting examples of such phenomena is important. Here we describe the emergence and spread of “tail walking”, an apparently arbitrary and non-functional behaviour, in a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

METHODS

The Port River estuary, on the southern coast of Australia (Figure 1), is home to a small (20-30, with transient visitors) community of *T. aduncus* [13]. Boat-based photo-identification studies of the dolphins in the Port River estuary commenced in 1988. Whenever dolphins were encountered, their location, number, and behaviour were recorded. Individuals were identified using distinguishing marks on their dorsal fins [14].

In addition, teams of up to five land-based, volunteer, citizen-scientists with experience observing and photographing the local dolphins documented behaviour using video and still images. Initially, these volunteers provided time-stamped photographs of dolphins tail walking, when observed, but in 2009 they were provided with a proforma collecting information on the dates and times of tail walk(s), the number of discrete tail walks observed, and the identity of the individual(s) concerned, if verified with dorsal photographs. Although parts of the river observed from land were approximately 200m across, individual identification was possible in 95% of cases. Unavoidably, due to its voluntary nature, observer effort varied during the course of the study.

A discrete tail walk was defined as the vertical emergence from the water of the dolphin so that at least two thirds of its body was above the water, followed by backwards movement through the water of at least a metre before submerging (Figure 2). Dolphins could perform a single tail walk in a day, bouts with successive tail walks separated by a few seconds, or multiple bouts within a single day separated by an hour or more. To accommodate this variability, we report 'DTW', the number of days in which tail walking was observed at least once, irrespective of the number of discrete tail walks performed, for each individual dolphin.

RESULTS

The first dolphin to be observed tail walking in the Port River estuary was Billie. This dolphin was photographed in the upper reaches of the Port River as a calf in the second half of 1987. On

December 26, 1987 Billie became trapped in a harbour and after two weeks, was captured and transferred to a nearby dolphinarium for rehabilitation. This facility housed five dolphins at the time, which were trained to perform various behaviours, including tail walking, in public shows. While being held, Billie was never given any training, but was able to observe the captive animals performing tail walks. She was subsequently freeze-branded on her dorsal fin, which allowed unambiguous re-identification after several years, and released near her capture site in late January 1988. Billie died in August 2009, with the precise date known because she was euthanised by veterinarians following recapture.

The first wild tail walk was observed in 1995, when Billie was estimated to have been about ten years old and thus an adult. Bouts of this behaviour were subsequently observed on a total of 279 occasions during the study period, resulting in 261 DTW [15]. Six adult females, and five juveniles (three female, two male) were observed tail walking (Table 1). The dolphin Wave accounted for a large majority of observations, 65-100% of the yearly DTW counts between 2007 and 2014. The frequency of Wave's tail walking increased rapidly during the period 2008 to 2010 (during which period Billie died). Wave was last seen on September 18 2014 and is presumed dead; and her male calf Tallula died in February 2015. Eight other dolphins were also observed tail walking during the period 2009-2014, but at a lower frequency (Table 1; Figure 3). Overall, 76% of tail walks occurred in the presence of other animals. Tail walking, as measured by DTW, peaked in 2010-11, and the total number of dolphins observed tail walking peaked in 2011 (Figure 3). After 2011, both DTW and the number of tail walkers declined.

All the identified dolphins observed tail walking were sighted regularly over several years (shaded cells in Table 1) and most were female; no adult male was ever observed tail walking. All tail walks occurred within the portion of the estuary shaded in Figure 1 in depths from 3m to 12m. Offshore areas were surveyed by boat on an approximately weekly basis [13], but no tail walking was observed there. The sighting ranges of all identified tail walkers overlapped considerably (Figure S1).

These ranges also overlapped with those of several animals, including three, Sparkle, TFM and Millie, which were never sighted tail walking, but all had calves that were observed tail walking (Figure S2, Tables S1-S2).

The observer effort involved in this study, totalling 30,620 hours, gradually increased from its inception in 1995 until it plateaued in 2006. Thus it is possible the amount of tail walking between these dates was greater than has been recorded. However, the relatively consistent observer effort from 2006 to 2014 indicates that the observed changes to the relative frequency of tail walking in this period are not an artefact of effort.

DISCUSSION

After being temporarily captive with other dolphins that had been trained to tail walk, Billie produced the behaviour in the wild, despite never receiving any direct training. This behaviour was subsequently produced by several other dolphins in the same community, particularly another female, Wave, leading to high production rates some 20 years after Billie's release into the wild. These high rates subsequently declined.

An obvious question is whether these changes in behaviour production were the product of social learning. We have only observational data, so any arguments must rely on plausibility, with all the associated caveats, such as the ease with which subtle genetic or ecological drivers can be missed [16]. Nonetheless, in this particular case, the plausibility arguments are unusually strong, for a number of reasons. First, the motor imitation capabilities of bottlenose dolphins are well established [17,18], so social learning has to be a candidate explanation for the spread of tail walking. Second is the arbitrary nature of the behaviour – it is a highly energetic display, so likely costly, that produces nothing energetically to offset that cost. It may produce social benefits, but these would be difficult to determine without intensive study. Third is the rarity of the behaviour in wild populations – while common in display performances in dolphinaria around the world, to our knowledge it does not appear in any ethogram of wild bottlenose dolphins. Fourth, the rise and fall of the production rate

120 of the behaviour only in some individuals and not the whole community is strongly suggestive of
121 social effects rather than, for example, a response to changing ecological conditions that would be
122 expected to produce a more consistent response across the community. Fifth, the observations
123 reported here are inconsistent with ecological or genetic causation. Tail walkers live in sympatry
124 with animals that have never been seen doing it, and tail walking individuals have both tail walking
125 mothers and mothers that have never been seen tail walking. Finally, there is a plausible route for
126 the introduction of this unusual behaviour, during Billie's temporary captivity. Given these
127 arguments, we conclude that the introduction and spread of tail walking in the Port River bottlenose
128 dolphin community is highly likely a result of social learning.

129 This report adds to our understanding of social learning in *Tursiops* spp.. The lack of obvious
130 adaptive benefits for tail walking contrasts with the vertical transmission of foraging specialisations
131 from mother to calf in other similar populations [19], and supports a social function for the
132 behaviour. There was also an apparent role of horizontal/oblique transmission to calves whose
133 mothers did not tail walk, with Wave the most likely source for learning events because of her high
134 rate of production. Behavioural synchrony for social function has hitherto been most prominent
135 within male alliances [20], but this report suggests a role in female-female interactions also.

136 Such observations help explain the large diversity of foraging strategies in bottlenose dolphins
137 [19,21,22], but the apparently arbitrary nature of tail walking behaviour is especially interesting
138 since such arbitrary traditions are much less common in non-humans, and we are not aware of any
139 other reports in this species. It is also striking that the behaviour was not produced at high rates until
140 a decade after it was originally introduced, showing that anthropogenic impacts on behaviour can
141 last for decades within populations, supporting the view that cultural transmission can be an
142 important consideration in conservation decisions [23,24].

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ACKNOWLEDGEMENTS

We are very grateful to the citizen scientists who provided much of the valuable data reported in this study, in particular Marianna Boorman, Barbara Saberton, Sharon Sharp and Jenni Wyrstra, and to Simon Allen and an anonymous reviewer whose comments improved the manuscript.

AUTHOR CONTRIBUTIONS

MB designed the study. MB, PB, AS, CF, JS and LR made substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data, to drafting and revising the article, and gave final approval of the version to be published. All authors approve the final version of the manuscript and agree to be held accountable for its content.

DATA ACCESSIBILITY

Data and code are available via the Open Science Foundation (https://osf.io/xjmdt/).

FUNDING

MB was supported by multiple grants from Whale & Dolphin Conservation (WDC).

COMPETING INTERESTS

All authors declare no competing interests

ETHICAL STATEMENT

Methods were observational only and adhered to local guidelines. Appropriate licences were obtained (SA Government research permit Q26490-2).

TABLES

Table 1: Days tail walking occurred (DTW) by individual and year. Shaded cells indicate years in which individuals were sighted.

Individual	Sex	1995	1998	2007	2008	2009	2010	2011	2012	2013	2014	Total
Billy	F	1	1		5	8						**15**
Wave	F			3	20	33	51	40	23	25	5	**200**
UAF*	F				1			1	1			**3**
Hope	M					1	2					**3**
Tallula	M						3	1				**4**
Bianca	F						6	5	1	3	1	**16**
Crinkle	F							3				**3**
Angel	F							2	1			**3**
Ripple	F							9	3			**12**
Ali	F							1				**1**
Melody	F										1	**1**
Total		**1**	**1**	**3**	**26**	**42**	**62**	**62**	**29**	**28**	**7**	**261**

*UAF = unidentified adult female. Given that this dolphin had no identifying features we cannot be certain that these three records are for the same animal.

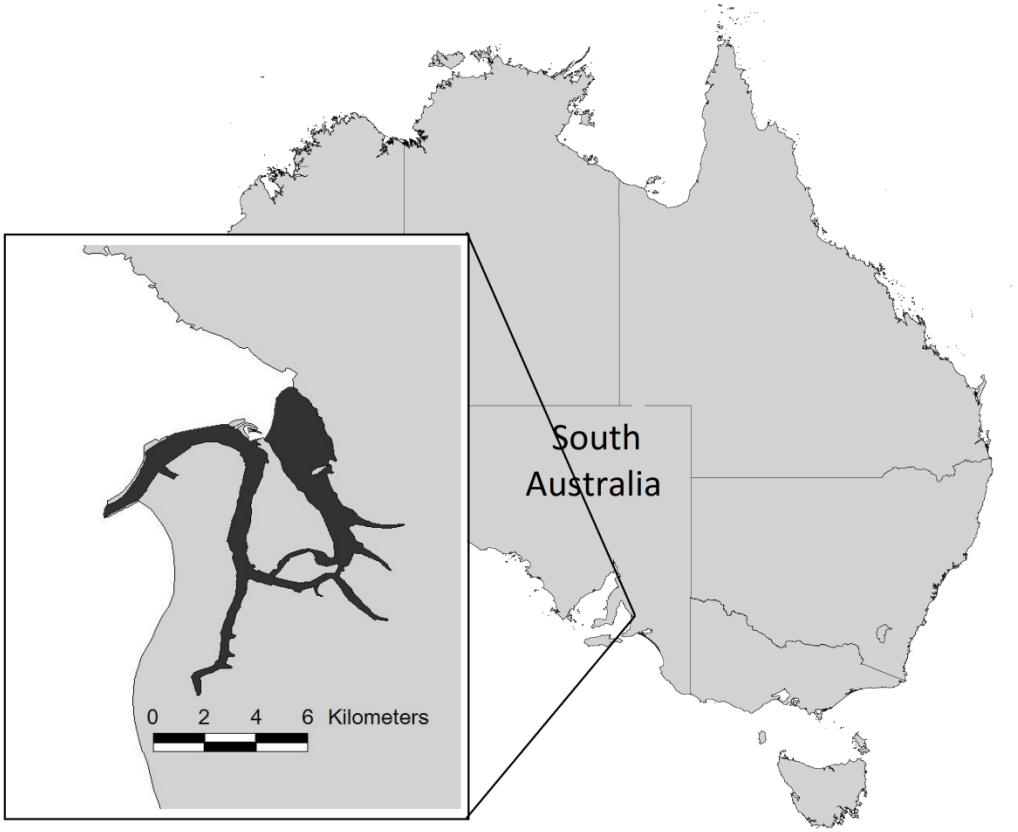
236 **FIGURE CAPTIONS**

237 Figure 1: Study area, the Port River estuary. The shaded area of the zoomed map encompasses all
238 the sightings of tail walking reported in the study.

239 Figure 2: (a) Adult female 'Wave' performing a typical tail walk – Note the backwards movements
240 through the water as indicated by the dolphin's wake, (b) Hours of observer effort, number of
241 individuals observed tail walking, and number of days tail walking observed (DTW) per 1000 hrs
242 observation effort, per year, across the study period. Asterisks indicate periods where DTW
243 occurred significantly more often than in the first five years of observation (see Supplementary
244 Material for modelling details).

245

246 FIGURE 1



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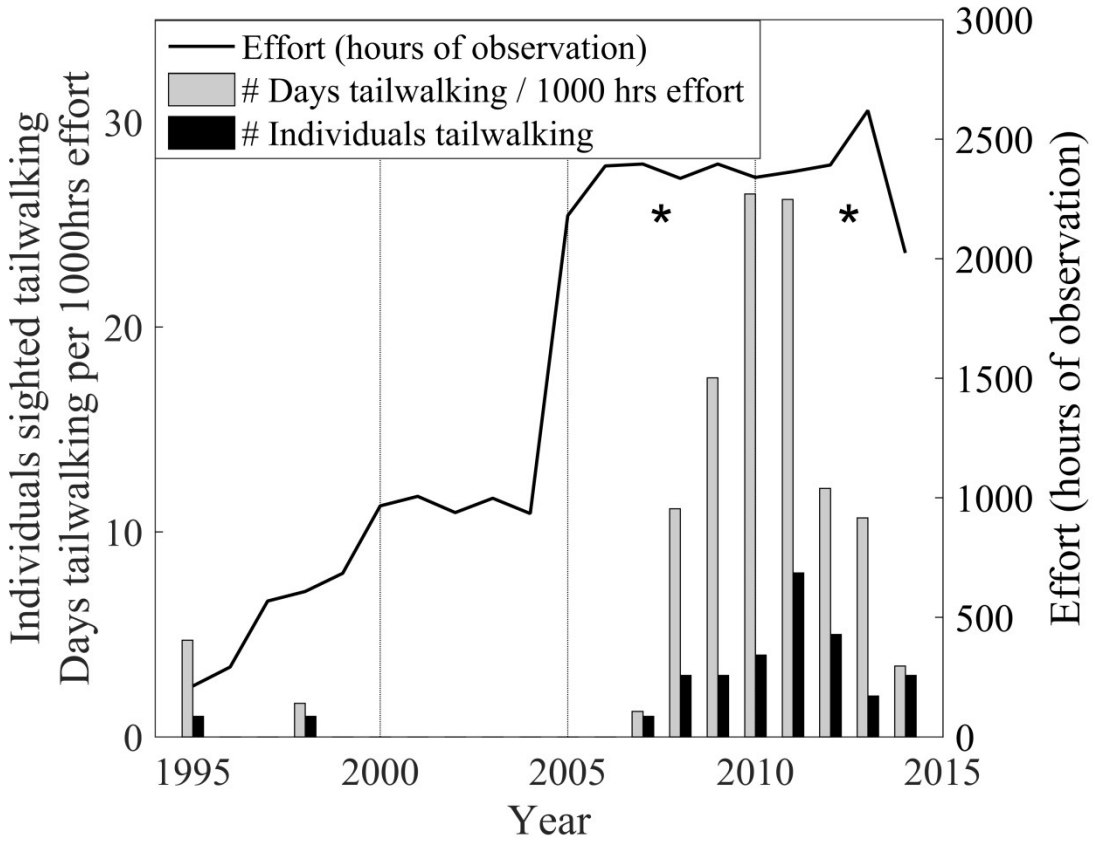
249 FIGURE 2

(a)

(b)



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SUPPLEMENTARY MATERIAL

FOR

Bossley, M., Steiner, A., Brakes, P., Shrimpton, J., Foster, C. and Rendell, L.: Tail walking in a bottlenose dolphin community: The rise and fall of an arbitrary cultural "fad", for *Biology Letters*

Table S1: Demographic details of tail walking dolphins.

NAME (Abbreviation in Figure S2)	SEX	EST. DoB
Billie (BI)	♀	1985 (first calf 1995)
Wave (WA)	♀	<1990 (first calf 2002)
Bianca (BIA)	♀	1992 (first calf 2002)
Unidentified Adult Female	♀	<1997
Crinkle (CR)	♀	<1980
Angel (AN)	♀	Dec, 2002
Ripple (RI)	♀	Jan, 2006
Melody (ME)	♀	Jan, 2006 (seen as neonate)
Hope (HO)	♂	Oct, 2008 (seen as neonate)
Tallula (TA)	♂	Mar, 2009 (seen as neonate)
Ali (ALI)	♀	Dec, 2010 (seen as neonate)

Table S2: Mother-calf relationships involving known tail walkers. Known tail walkers in bold; all animals are female unless otherwise indicated.

Mother:	**Wave**		**Bianca**	Sparkle	Millie	TFM
	↓	↓	↓	↓	↓	↓
Calf:	**Ripple**	**Tallula (♂)**	**Hope (♂)**	**Melody**	**Ali**	**Angel**

Table S3: Results of Poisson family GLM fitted to effort-corrected DTW time series binned into four 5-year epochs: (model1<-glm(TW~epoch1, family = 'poisson'))

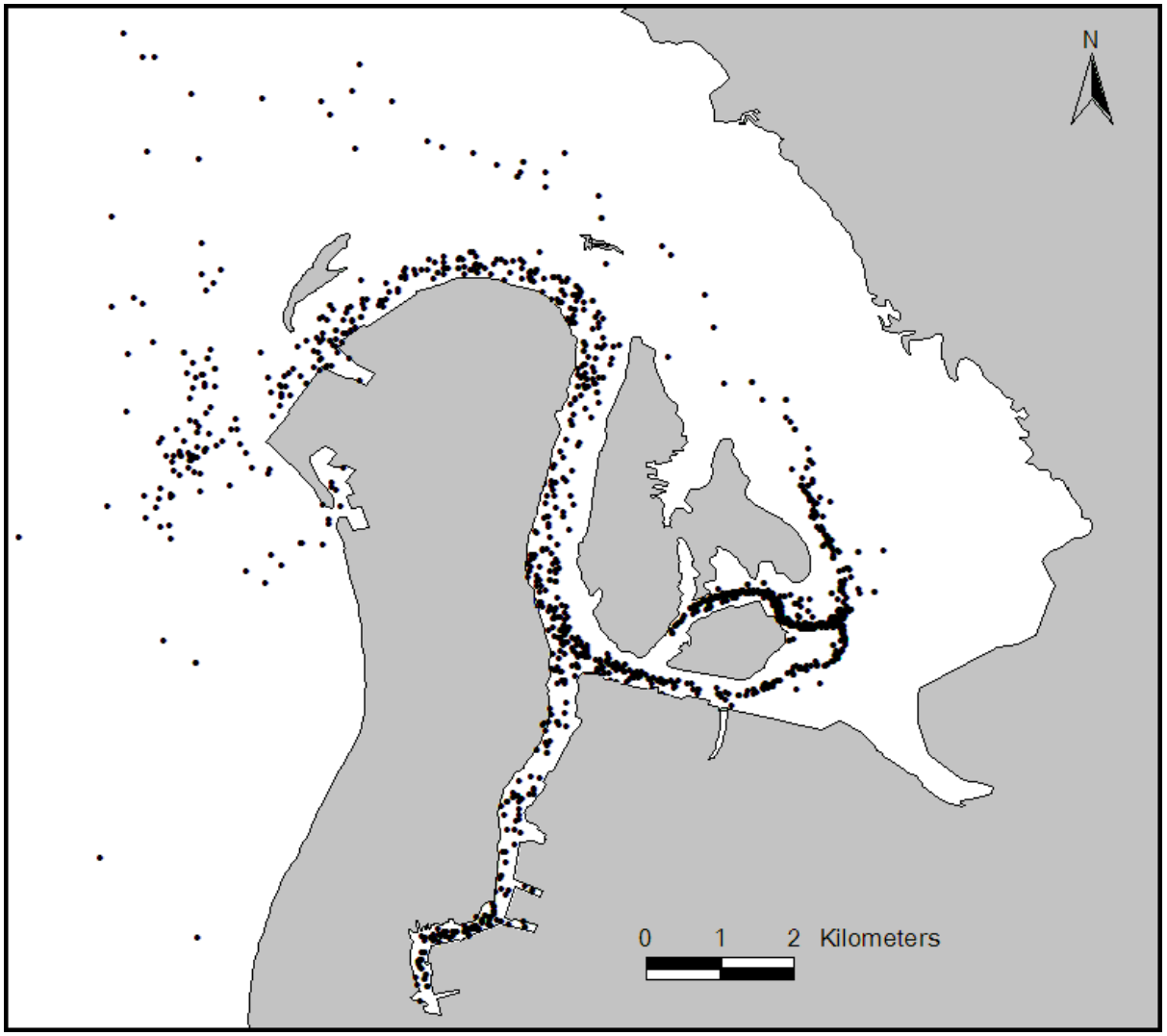
Coefficient	Estimate	Std.Error	z	Pr(>|z|)
Intercept (1995-1999)	0.24	0.40	0.608	0.5435
2000-2004	-17.54	1550.87	-0.011	0.9910
2005-2009	1.55	0.44	3.545	0.0004
2010-2014	2.52	0.41	6.112	9.82e-10

Null deviance: 231.830 on 19 degrees of freedom

Residual deviance: 89.506 on 16 degrees of freedom

Figure S1: Locations of boat-based survey sightings of (a) known tail walking animals and (b) individuals never seen tail walking, to illustrate the overlapping ranges of both.

(a)



280 **(b)**

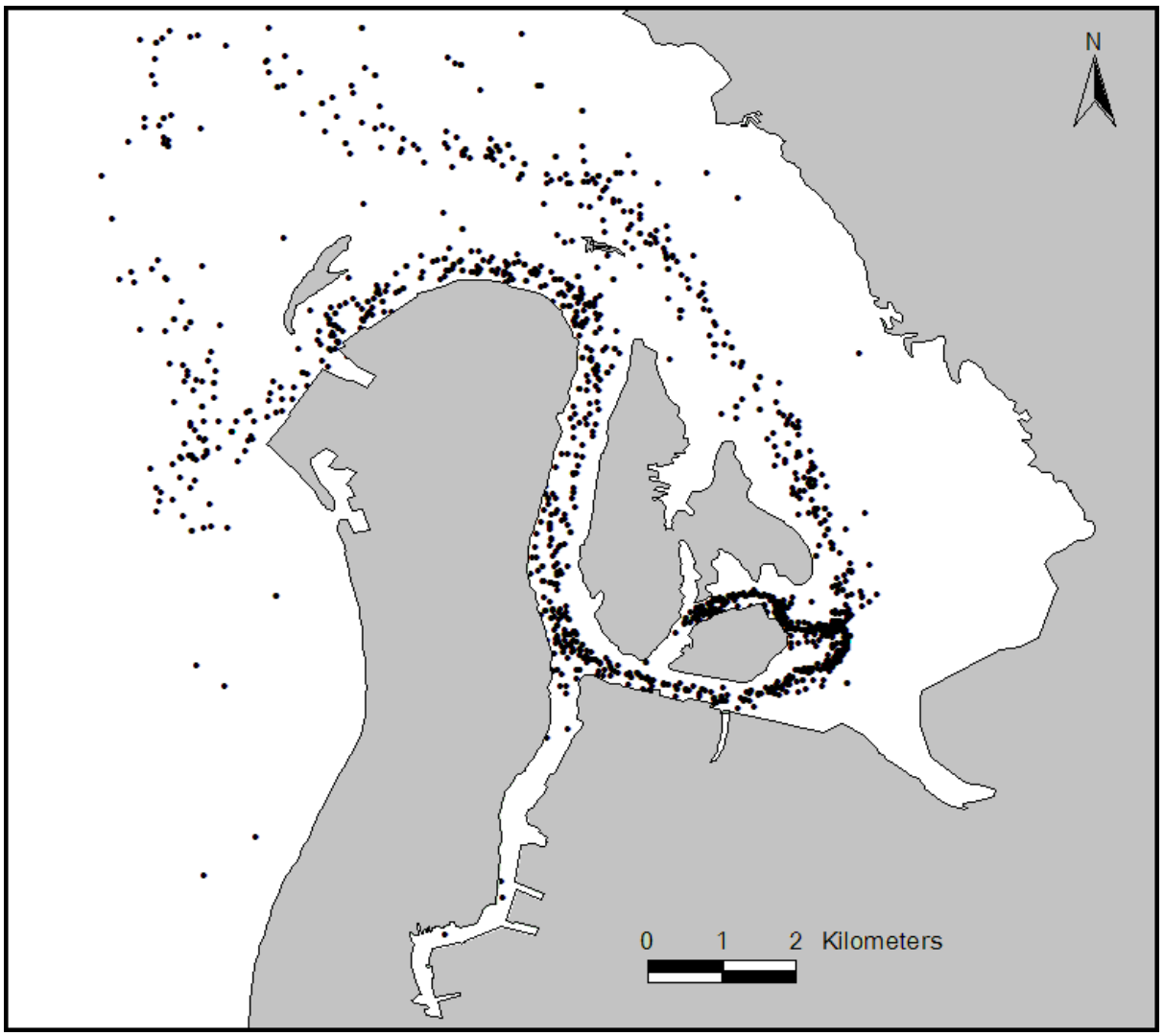


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Figure S2: Distribution of number of tail walk events in each observed bout, by individual, presented as standard boxplots (see Table S1 for full individual names).